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Description of a new species of *Parasphena* Bolivar, 1884 (Orthoptera: Pyrgomorphidae) from northwestern Tanzania and new data on the biogeography, coenology, habitat and morphology of the genus

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Abstract

A new species of *Parasphena* is described from southwestern Tanzania, occurring in the montane zone of the third highest mountain, Mt Hanang. Morphological details are given for *P. hanangensis* n. sp. and for species on the northern branch of the Eastern Arc mountains, Mt Kilimanjaro and the Kenyan highlands, morphologically related to this new species. A coenological comparison is made between several high mountains of East Africa; patterns of present-day distribution — the result of climatic fluctuations of the past — are discussed. Information on distribution, habitat and altitudinal ranges are given for all species of the genus *Parasphena*.

Key words

Parasphena, new species, distribution, speciation, Mt Hanang, East Africa

Introduction

East African high mountains are well-known hotspots of diversity and endemism (Fjeldså & Lovett 1997, Burgess *et al.* 2007, Hemp 2007). Especially in the group Saltatoria, several flightless genera show arrays of closely related species, mostly inhabiting the montane zones of high mountains or mountainous areas. For some lentulid genera these species swarms are obviously the result of allopatric speciation, as *e.g.*, shown for the genus *Rhainopomma*—occurring on the geologically old mountains of the so-called Eastern Arc mountains of Tanzania and southern Kenya—or *Usambilla*, also with its center of diversity in Tanzania (Hemp *et al.* 2007, Schultz *et al.* 2007). To further illuminate modes and times of speciation of flightless Saltatoria taxa in East Africa, the genus *Parasphena* was investigated and data on distribution and habitat recorded.

The genus *Parasphena* was erected by Bolivar in 1884, based on *Sphenarium pulchripes* from Kilimanjaro, originally described by Gerstäcker 1869. Kevan (1948) revised *Parasphena* and described several new species. Kevan (1956) revised the group again and subdivided the genus *Parasphena* into several genera, based on characters such as the presence of vestigial tegmina, the shape of the frons of the head or general body shape. Kevan (1956) stated that the generic distinctions are rather fine and probably artificial.

Parasphena is characterized as being completely apterous with fairly distinct carinae of the pronotum, an apically parabolic fastigium and a thorax which is not notably broad, short or depressed. Some of the newly erected genera are closely related to *Parasphena*, *e.g.*, *Afrosphenella*, *Parasphenella*, *Parasphenula*, or *Stenoscepa*.

Dirsh (1961) synonymized several genera erected previously by Kevan (1956) on *Parasphena* spp. (*Afrosphenella*, *Parasphenoides*,

Parasphenula) with *Stenoscepa*. He also incorporated several species still under *Parasphena* into *Stenoscepa*.

At present 16 species of *Parasphena* are known (Eades & Otte 2008). *Parasphena* has its greatest diversity in East Africa, with most species occurring on isolated high mountains in the area of the Kenyan highlands and northern Tanzania. The aim of the present paper is to describe a new species of *Parasphena* and to provide data on the distribution and habitat of this genus.

Material and Methods

Images.—The images of *Parasphena* species were taken from collection material of NHML. Paratypes or the holotype were chosen for documentation of characters of *Parasphena cherenganica*, *chyuluensis*, *kaburu*, *keniensis rehni*, *kinangopa*, *kualensis*, *mauensis*, *kamasiensis*, *mauensis mauensis*, *meruensis zeuneri*, *nairobiensis*, *naivashensis*, *ngongensis*, *teitensis* and *pulchripes*. For *P. campestris*, *elgonensis*, *imatongensis*, *keniensis keniensis* and *meruensis meruensis* — specimens identified by Kevan were investigated. Additionally, material collected from the field was studied: *P. pulchripes*, *P. meruensis* ssp., *P. teitensis*, *P. chyuluensis*, *P. keniensis* ssp., *P. nairobiensis*, *P. kinangopa*, and *P. ngongensis*.

Measurements.—Total body length, dorsal aspect, refers to the midline length of the insect from fastigium verticis to abdomen tip.

Depositories.—MNB: Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin. NHML: Natural History Museum London, UK. EDNMK: Entomological Department National Museums of Kenya, Nairobi. All other material remains in the collection of C. Hemp.

Results

Parasphena hanangensis Hemp C. n. sp.

Holotype.—Male, Tanzania, southern slope of Mt. Hanang, 2600 m, montane grassland, UTM zone 36 M 9506496E 0765425S, 1/08, depository: MNB.

Paratypes.—1 female, same data as holotype, depository: MNB. 1 male, 1 female, same data as holotype, depository: NHML. 1 male, 1 female, same data as holotype, depository: EDNMK. Further paratype material studied: 17 males, 8 females, same data as holotype. 1 male and 1 female, near top of Mt. Hanang, montane grassland, 3400 m 1/08.

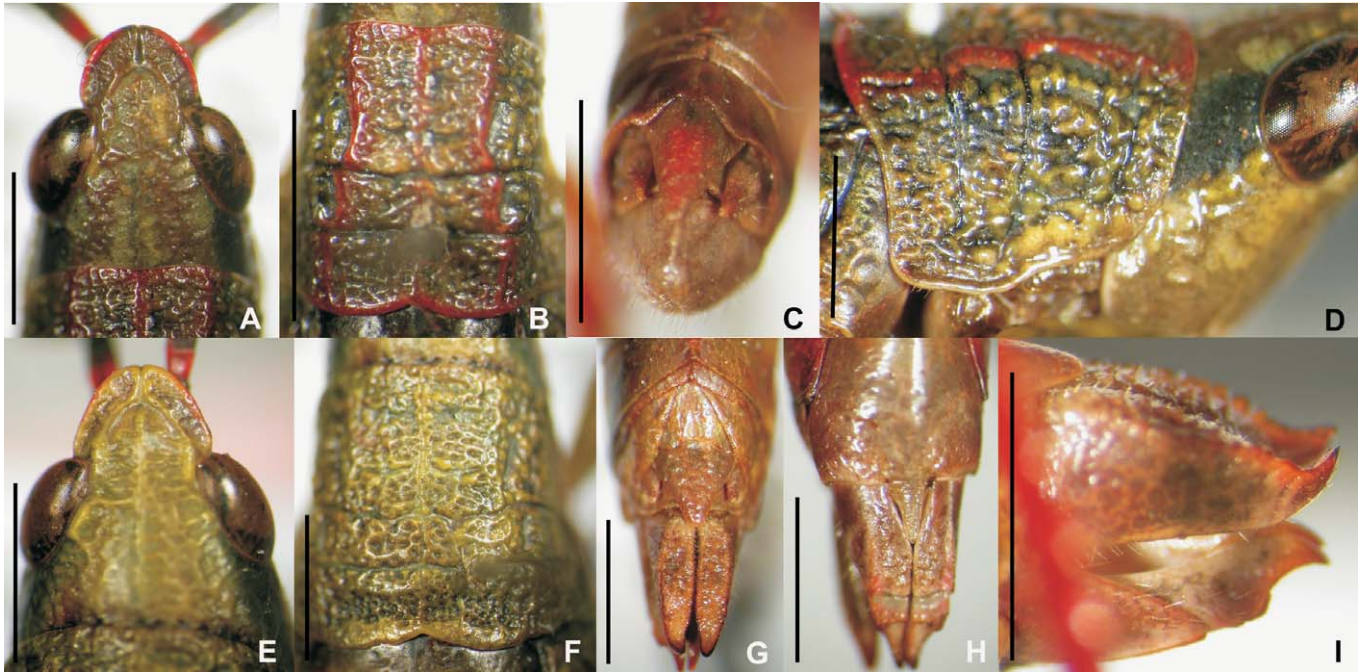


Fig. 1. *Parasphena hanganensis*. Male (A-D); Female (E-I). A: male head dorsal aspect showing fastigium; B: dorsal view of male pronotum; C: dorsal view male abdomen apex; D: lateral view of male pronotum. E: female head, dorsal aspect with fastigium; F: female pronotum, dorsal aspect; G: dorsal view, female abdomen apex showing dorsal valves; H: ventral female abdomen apex showing ventral valves; I: lateral aspect of female abdomen apex (scale bars 2 mm). For color versions, see Plate IV.

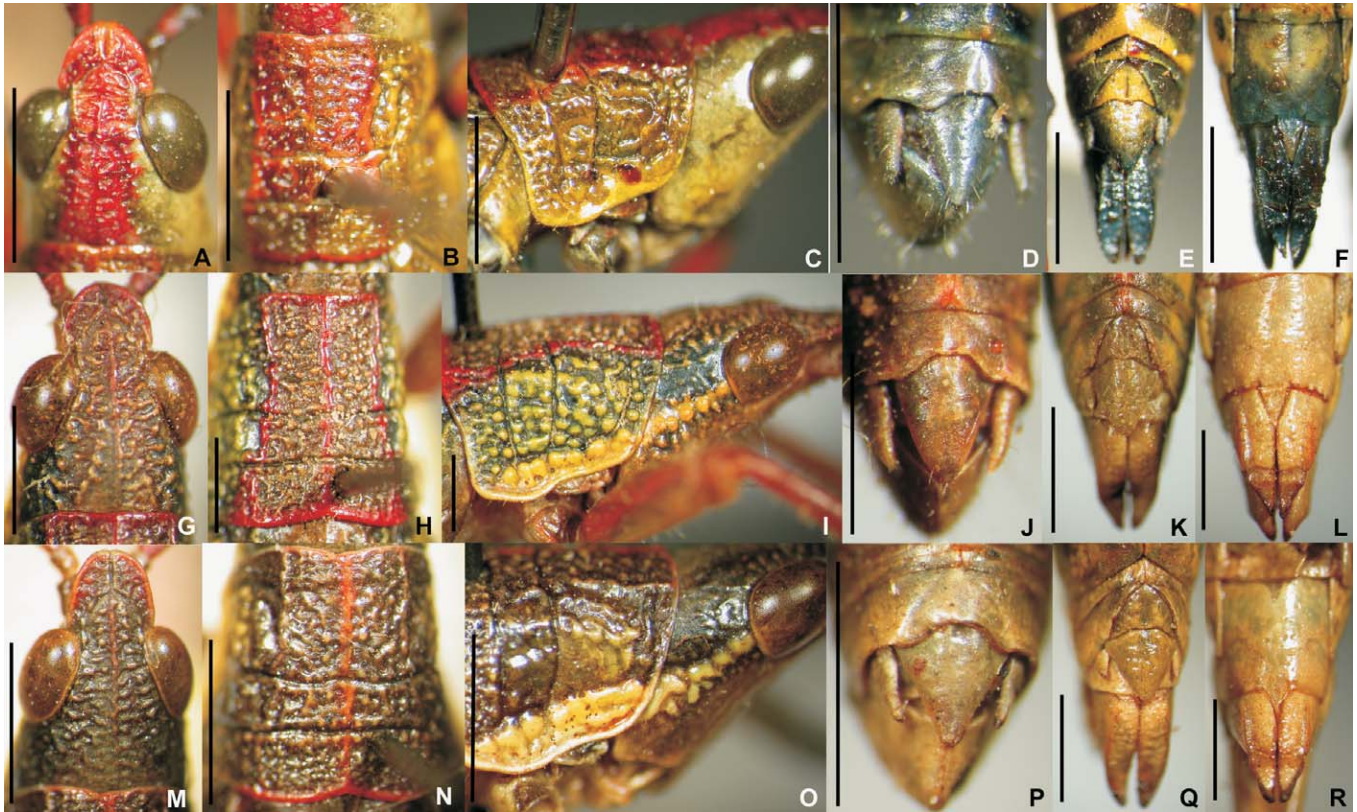


Fig. 2. *Parasphena* species morphologically related to *P. hanangensis*. A-F, *P. pulchripes*. A: male head, dorsal aspect; B: male pronotum, dorsal view; C: male pronotum, lateral view; D: male abdomen apex; E: female abdomen apex, dorsal view; F: female abdomen apex, ventral view. G-L, *P. teitensis*. G: male head dorsal; H: male pronotum, dorsal; I: male pronotum, lateral; J: male abdomen apex, dorsal view; K: female abdomen apex, dorsal view; L: female abdomen apex, ventral view. M-R, *P. chyuluensis*. M: male head dorsal; N: male pronotum, dorsal; O: male pronotum, lateral; P: male abdomen apex, dorsal; Q: female abdomen apex, dorsal view; R: female abdomen apex, ventral view (scale 2 mm). For color versions, see Plate V.

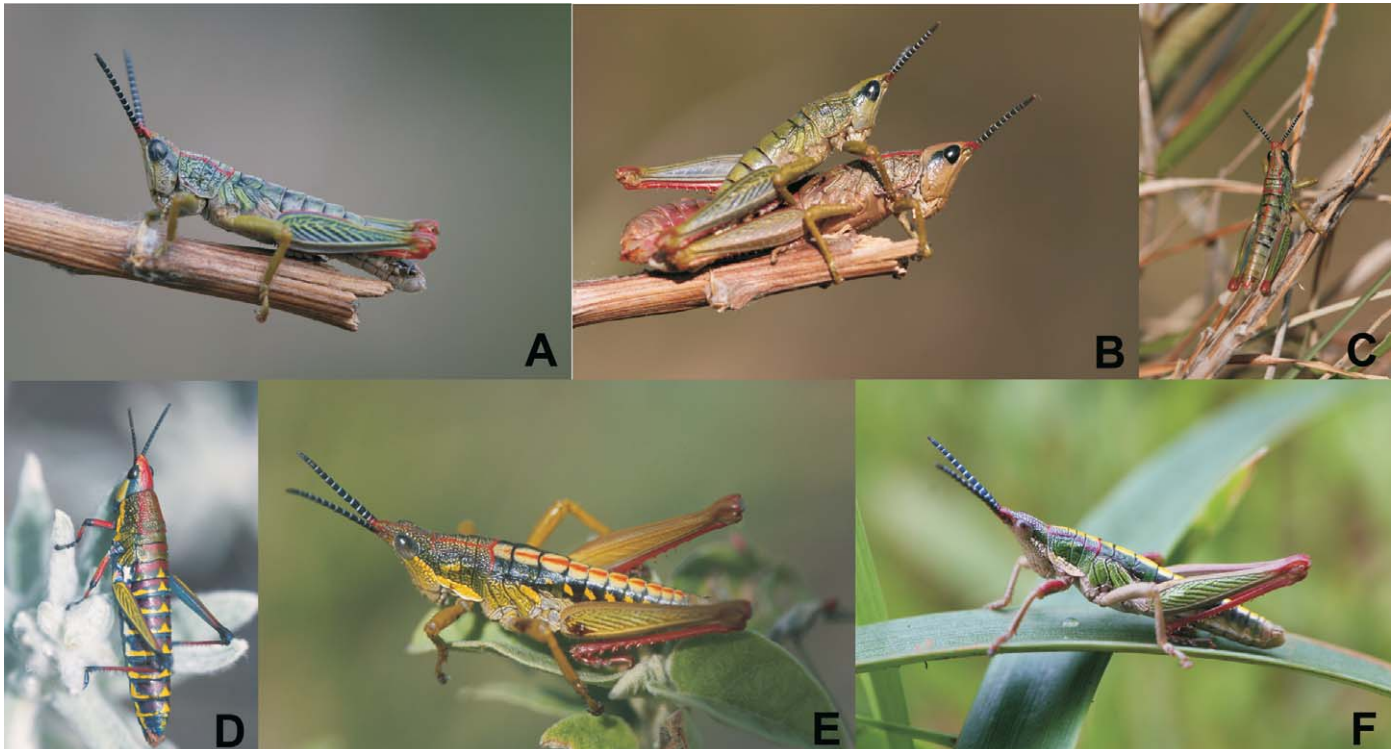


Fig. 3. A-C, *Parasphena hanangensis* field photos of specimens in montane grassland on southern slopes of Mt Hanang at 2650 m. A: male. B: copulating pair. C: male, dorsal aspect. D: female *P. pulchripes* on *Senecio* sp. at 2700 m in moorland zone above Maua, Mt Kilimanjaro, southern slopes, Tanzania. E: male *P. chyluensis*, 1950 m, northern side of the Chyulu Hills, Kenya. F: male *P. nairobiensis* (savanna grassland) at 1700 m on the lower southern slopes of Ngong Hills, beside the road Kiserian-Isinya, Kenya. For color versions, see Plate V.

Description. — **Male.** Color: predominant color of living insect blue-green, with red lines on pronotum, reddish areas on hind femora and fastigium verticis; tibiae red-orange (Fig. 3A-C). Preserved insect olive-green, red on fastigium verticis (Fig. 1A), on carinae of pronotum (Fig. 1B) and on hind tibiae.

Head and antennae: antennae typical for genus, slightly shorter than head and pronotum together; first and second antennal segment dark red; frontal ridge sulcate throughout; basal width of fastigium verticis $1.3 \times$ greater than length; lateral margins red. Furcula of fastigium well developed. Median carina of head distinct throughout; granules of cheek dirty yellow or absent; in living insect a conspicuous dark band begins at posterior eye margin, running to anterior margin of pronotum (Fig. 3A-C); in preserved insect this band faded; face greenish.

Thorax: pronotum slightly broader than long; pronotal disc with granules on pro- and mesozona; on metazona granules more evenly distributed; median and lateral carinae of pronotum well developed, red colored; lateral carinae converging in prozona, diverging in meso- and metazona (Fig. 1B); lateral lobes similarly textured as pronotal disc (Fig. 1D), granules of lower margins not arranged in any distinct row; first pronotal sulcus crossing lateral lobes, but not crossing pronotal disc; second and third sulcus well developed, continuous; second sulcus crossing at about center of pronotum; interstitial sulcus present. Posterior margin of pronotum shaped by shallow midline excision into two broadly convex halves lined red; prozona as long as meso- and metazona of pronotum taken together (Fig. 1B); prosternal tubercle low; mesosternal interspace almost square.

Legs: in preserved insect uniformly olive-green, joints yellowish; lunules of hind femora brown-reddish; outer side of hind femora

with a pattern of olive green and faded bluish stripes arranged in a parallel fashion; in living insect especially the outer side of hind femora, more vividly blue and green, upper half intermingled with yellow (upper margin of hind femur in some specimens lined red); lunules of knees red-brown; inner sides of femora partly blue.

Abdomen: abdominal terga smooth shiny, with only a few minute scattered punctures, especially on 1st and 2nd tergites (in preserved insects abdomen of uniformly dark olive green to red brown without any pattern); in the living specimen abdomen olive green, posterior parts of sternites with black markings of variable extent (in some specimens a dark red central line is present); tips of abdomen red; cerci conical, laterally slightly compressed, ending before tip of supra-anal plate; subgenital plate with blunt knob-like apex, supra-anal plate triangular (Fig. 1C).

Female: larger and stouter than male (Figs 1E-I, Fig. 3B). Color in living specimens not so contrasting as in males, but principally same color patterns as for male holotype. Preserved females brown to green with red orange hind tibiae. Pair of lateral fasciae on cheeks as in male, black. Cerci very broad at base, laterally compressed, about half as long as supra-anal plate (Fig. 1G). Exposed area of dorsal valves are on average 1.1 mm broad and 2.2 mm long, thus very stout (Fig. 1I). Dorsal surface of dorsal valves sculptured (Fig. 1G), the tips up-curved sclerotized; ventral valves as visible beyond margin of subgenital plate are only 1 mm long, the tips sclerotized and down-curved (Fig. 1H, I).

Measurements.— All measures in mm.

| | males n = 10 | females n = 10 |
|------------------------|-------------------------------|------------------------------|
| head width | 2.5-3.0 (\bar{x} = 2.8) | 2.9-3.4 (\bar{x} = 3.3) |
| inter-ocular distance | 1.0-1.2 (\bar{x} = 1.05) | 1.2-1.6 (\bar{x} = 1.5) |
| pronotum | 3.1-3.7 (\bar{x} = 3.3) | 3.7-4.6 (\bar{x} = 4.2) |
| posterior femur length | 9.0-10.8 (\bar{x} = 10.2) | 9.5-11.2 (\bar{x} = 10.4) |
| posterior femur depth | 2.0-2.4 (\bar{x} = 2.3) | 1.8-2.5 (\bar{x} = 2.2) |
| total body length | 18.0-23.0 (\bar{x} = 21.2) | 23-30 (\bar{x} = 26.6) |

Diagnosis.— A large species, both sexes having similar dimensions as, e.g., *P. chyuluensis*, with comparatively little sexual dimorphism. Generally it belongs to *Parasphena* species characterized by a comparatively broad fastigium (Figs 1A, 2A, G, M), a male pronotum with clearly marked (also in color) median and lateral carinae (Figs 1B, 2B, H, N), and in males an angularly excised terminal abdominal tergite, which is medially slightly uplifted and notched, and stout cerci which are shorter than the supra-anal plate (Figs 1C, 2D, J, P).

The females of this morphological group have stout valves, the dorsal one sculptured and the dorsal surface slightly inflated (Figs 1G, 2E, K, Q), while the ventral valves have two levels at their posterior part and small, down-curved apices (Figs 1H, 2F, L, R). These characters are found in *P. pulchripes* from Mt Kilimanjaro, *P. teitensis* from the Taita Hills, *P. chyuluensis* from the Chyulu Hills. They are similarly found in *P. nairobiensis* from around Nairobi, the lower Ngong Hills and the Machakos area of Kenya and in *P. campestris* from Mt Kenya (unfortunately the specimens of *P. campestris* seen in the NHML seem to have been discolored in alcohol). In Fig. 2, *P. pulchripes*, *P. teitensis*, and *P. chyuluensis* are shown for comparison of these characters.

The color pattern of *Parasphena* seems to vary little within species and thus seems a good character for their identification. In the species listed above, a dark to black band, from behind the eyes running to the anterior margin of the pronotum, is very typical and very conspicuous, especially in *P. hanangensis* (Figs 1D, 3A-C). This band is present in the majority of specimens including *P. pulchripes* (Fig. 3D), *P. chyuluensis* (Figs 2O, 3E), *P. teitensis* (Fig. 2I), and *P. nairobiensis* (Fig. 3F). All other *Parasphena* species lack this black band, excepting *P. elgonensis*. However, *P. elgonensis* seems to be a generally dark-pigmented species, the whole genae and dorsal surface of the head being blackish, hence a black band as such not being defined. As mentioned above, investigated *P. campestris* specimens which could also exhibit this character, since otherwise morphologically related to this group, were probably discolored.

Morphologically *P. hanangensis* is most closely related to *P. pulchripes* from Mt Kilimanjaro. The two species also occupy a similar habitat — montane (afro-alpine) grass and bushlands — on two of the highest mountains of Tanzania. As in *P. pulchripes* and in contrast to the other two related species (Fig. 2C, I, O), *P. hanangensis* does not have a row of granules along the lower margin of the pronotal lobes. Also the genae are more or less smooth. These structures are also very reduced in *P. pulchripes* (Fig. 2C) and *P. campestris*. Nor does *P. keniensis rehni* show these structures. In *P. imatongensis* granules are present, but scarcely arranged as bands and in *P. kulalensis* granules are present on the genae, also not arranged as a band. In most other *Parasphena* species these granules are present on the lower margin of the pronotal lobes and the genae and are often a conspicuous row of (partly) large granules marked in color (mostly yellow or whitish).

Differences to *P. pulchripes* are found in general color pattern: *P. pulchripes* is the most colorful *Parasphena* species (Fig. 3D), while *P.*

hanangensis is a more uniformly bluish-greenish color. The lunules of the leg joints are red-brown in *P. hanangensis* (Fig. 3A-C), while they are black in *P. pulchripes* (Fig. 3D). Furthermore, sexual size dimorphism is very marked in *P. pulchripes*, males being very tiny, while their females are among the largest of all *Parasphena* species, (*P. pulchripes* females on average being 1.8 times larger than males; 5 measured males and females). In *P. hanangensis* females are only slightly larger than males, especially when not carrying eggs (on average females being 1.25 times larger than males). The female of *P. pulchripes* from Kilimanjaro has ovipositor valves very similar to *P. hanangensis*. However, in *P. pulchripes* the surface is strongly sculptured with large elevated tubercles, while in *P. hanangensis* the tubercles of this area are not as large as in *P. pulchripes* (Fig. 1G, H and Fig. 2E, F). Another difference is the color — deep black in *P. pulchripes* and brown in *P. hanangensis*.

Distribution.— So far, *P. hanangensis* is only known from the type locality of montane grasslands of Mt Hanang in northwestern Tanzania. Table 1 gives information about distribution, habitat and altitudinal ranges of the 17 *Parasphena* species known at present.

Co-occurring Saltatoria species.—Saltatoria species co-occurring with *P. hanangensis* were noted on two montane grasslands on the southern slopes of Mt Hanang. One is a recently burnt area with former *Erica* bushland intermingled with grasslands in regeneration at 2600 m and the second an open grassland at the same elevation.

On the burnt-bush grassland *Hadrolecocatantops kilimandjaricus* (Ramme, 1929), *Heteropternis coulöniana* (Saussure, 1884), *Parepistaurus* sp. and *Phlesirtes* sp. occurred. On the open grassland *Coryphosima stenoptera* (Schaum, 1853) was very frequent. Further grassland species were *Parepistaurus* sp. and *Altihoratosphaga hanangensis* (Hemp et al. 2009 b).

The Saltatoria composition of Mt Hanang at this altitude corresponds well with coenoses found on other high mountains in East Africa at this elevation. Very typical are *Coryphosima stenoptera* and *Heteropternis coulöniana*. These two species have a high altitudinal range on mountains from submontane to afro-alpine habitats (Hemp & Hemp 2003). Restricted to the high montane and alpine zone are species of the genera *Parasphena*, *Phlesirtes*, and *Uganda* (Table 2). Typical open-land inhabitants of the montane zone are e.g., *Hadrolecocatantops kilimandjaricus*, *Gymnbothroides*, and *Altihoratosphaga* species. *Parepistaurus* species are usually dwellers of herb vegetation of forest edges and clearings of the lower montane and submontane zones of mountains. On Mt. Hanang single *Parepistaurus* individuals of a yet-undescribed species were found exceptionally high up, perhaps having “climbed” up the mountain in the hot season of the year.

Discussion

Parasphena is a genus distributed in the highlands of Kenya and northern to northwestern Tanzania (see map, Fig. 4). Most of the Parasphenina (Kevan & Akbar 1964) are restricted to the montane zone, occurring today on isolated high mountains and mountain ranges in tropical Africa and the Arabian Peninsula. To the north and the south, *Parasphena* is replaced by species of Parasphenina still retaining wings (though these are reduced), species of genera such as *Stenoscepa* or *Parasphenula*, part of which were originally described as *Parasphena*. Kevan (1948) noted that the trend towards the apterous condition has proceeded further in the central zone of the distribution area of this group than in either the north or the

Table 1. Distribution, habitat and altitudinal range of *Parasphena* species.

| | Distribution | Habitat | Altitude |
|--|---|--|--|
| <i>P. campestris</i> Rehn, 1942 | Nanyuki-Naromoru, western side of Mt Kenya, Kenya | montane shrub and grassland** | 1800m (Rehn 1942) |
| <i>P. cheranganica</i> Uvarov, 1938 | Cherengani Hills, Kenya | montane grasslands** | 2500-3500m (Rehn 1942, Uvarov 1938) |
| <i>P. chyuluensis</i> Kevan, 1948 | Chyulu Hills, Kenya | montane grasslands and low shrub vegetation | 1650-2200m (Kevan 1948 & own data) |
| <i>P. elgonensis</i> Sjöstedt, 1933 | Mt Elgon, Kenya | heath zone ** | 2500-3500m** (Rehn 1942, Uvarov 1938) |
| <i>P. hanangensis</i> n. sp. | Mt Hanang, Tanzania | montane grasslands and low shrub vegetation | 2600-3400m |
| <i>P. imatongensis</i> Rehn, 1942 | Imatong Mts, Sudan | montane grasslands** | 2400**-3200m (Rehn 1942) |
| <i>P. kaburu</i> Kevan, 1948 | Eldoret, Kenya | montane grasslands and low shrub vegetation | 2000m (Kevan 1948) |
| <i>P. keniensis keniensis</i> Sjöstedt, 1912 | Mt Kenya, Kenya | forest clearings & montane grassland, moorlands | 1900-3000m |
| <i>P. keniensis rehni</i> Kevan, 1956 | Kikuyu Escarpment, Kijabe, Kenya | montane grasslands and low shrub vegetation | 2100-2600m (Kevan 1956 & own data) |
| <i>P. kinangopa</i> Uvarov, 1938 | Aberdare Range, Kenya | montane grasslands and low shrub vegetation, moorlands and <i>Helichrysum</i> vegetation | 2400-4000m (Rehn 1942, Uvarov 1938 & own data) |
| <i>P. kulalensis</i> Kevan, 1956 | Mt Kulal, Kenya | ? | 1650-2000m (Kevan 1956) |
| <i>P. mauensis kamasiensis</i> Kevan, 1948 | Kamasia Hills, Kabarnet, Kenya | montane grasslands and low shrub vegetation** | 2150m (Kevan 1948) |
| <i>P. mauensis mauensis</i> Kevan, 1948 | Kericho, Mau summit, Londiani, Kakamega, South Kavirondo, Kenya | montane grasslands and low shrub vegetation | 1200-2600m (Kevan 1948, 1956 & own data) |
| <i>P. meruensis meruensis</i> Sjöstedt, 1909 | Kampala, Tororo Hills, Uganda Mts Kilimanjaro and Meru, Tanzania | montane grassland | Mt. Meru: 1700*-4000m (Sjöstedt 1909) |
| <i>P. meruensis zeuneri</i> Kevan, 1956 | Ngorongoro conservation area, Tanzania | montane grasslands and low shrub vegetation | Mt. Kilimanjaro 1700-2500m |
| <i>P. nairobiensis</i> Sjöstedt, 1933 | plains between Nairobi, Ngong Hills and Kajiado, Mt Machakos | montane grasslands and low shrub vegetation | 1600-2800m (Kevan 1956 & own data) |
| <i>P. naivashensis</i> Kevan, 1948 | Rift valley between Nakuru and Lake Naivasha, Kenya | montane grassland | 1700-2100m |
| <i>P. ngongensis</i> Kevan, 1948 | Ngong Hills, Kenya | montane grasslands and low shrub vegetation | 1900m (Kevan 1948) |
| <i>P. pulchripes</i> (Gerstaecker, 1869) | Mt Kilimanjaro, Tanzania | <i>Erica</i> region (Sjöstedt 1909) <i>Helichrysum</i> shrub vegetation, moorland zone (tussock grasslands) | 2100-2400m |
| <i>P. teitensis</i> Kevan, 1948 | Taita Hills, Kenya | montane grasslands and low shrub vegetation | 2400-4400m (Sjöstedt 1909, Rehn 1942 & own data) |
| | | | 1350-1950m (Kevan 1948 & own data) |

* Sjöstedt states that *P. meruensis meruensis* is found from elevations of the so-called "Meruniederung", in the cultivation belt and the rain forest. Thus it probably occurs, as on Mt. Kilimanjaro, from 1700 m upward.

** information taken from specimens in the collection of the NHML

Table 2. Species and mountain/range associations. H: Mt Hanang (2600 m); Ki: Mt Kilimanjaro (2600 m); M: Mt Meru; No: Ngorongoro (2200 m); ME: Manyara Escarpment, Nou forest reserve (2100 m); Ng: Ngong Hills (2100 m); C: Chyulu Hills* (1900 m); A: Aberdare Range (2900 m); Ke: Mt Kenya (3000 m); fl: flightless species; en: endemics to respective mountain.

| Species / mountain | H | Ki | M | No | ME | Ng | C | A | Ke | fl | en |
|---|---|----|---|----|----|----|---|---|----|----|----|
| <i>Coryphosima stenoptera</i> (Schaum, 1853) | x | x | x | x | x | x | x | x | x | | |
| <i>Heteropternis coulouiana</i> (Saussure, 1884) | x | x | x | x | x | x | x | x | x | | |
| <i>Hadrolecatantops kilimandjaricus</i> (Ramme, 1929) | x | x | x | | | | x | | | | |
| <i>Parasphena</i> sp. Bolivar, 1884 | x | x | x | x | | x | x | x | x | x | x |
| <i>Phlesirtes</i> sp. Bolivar, 1922 | x | x | x | x | x | x | x | x | x | x | x |
| <i>Pezocatantops</i> sp. Dirsh, 1953 | | | | | | x | | x | x | x | x |
| <i>Uganda</i> sp. Bolivar, 1909 | | x | | | | | | x | | x | x |
| <i>Gymnbothroides</i> sp. Karny, 1915 | x | x | x | x | x | x | x | x | x | x | ? |
| <i>Altihoratosphaga</i> sp. Hemp, 2009 | x | | x | x | x | | | | | x | x |

* Because of the lower elevation, the plot yielded more species which are not listed here.

south.

Species of the genus *Parasphena* are morphologically homogenous, suggesting a very close relationship and a geologically quite recent origin. Rehn (1942) noted that "*Parasphena* was more continuously distributed during Pleistocene times. The comparatively close affinity of the components of certain of the East African aggregations points quite definitely to a relatively recent segregation of populations of older species, which may have taken place as recently as the Post-Pleistocene."

Preliminary investigations of some of the species (*P. kinangopa*, *P. meruensis meruensis*, *P. ngongensis*, *P. pulchripes*, *P. keniensis rehni*, *P. keniensis keniensis*, *P. chyuluensis*, *P. nairobiensis*) underline this suggestion, since molecular analyses of the more conservative genes, Histon and the faster-evolving gene COI, showed that the investigated *Parasphena* species could not be separated (Pernat 2007 unpubl.). Morphologically, a closer relationship is suggested between *P. campestris*, *P. nairobiensis*, *P. chyuluensis*, *P. teitensis*, *P. pulchripes* and *P. hanangensis* (see Figs 1, 2), all occurring in adjacent high mountains or mountain ranges. Particularly *P. pulchripes* and *P. hanangensis* seem to be very closely related (see under diagnosis). Mt Kilimanjaro and the highlands west of the rift valley also share several other Saltatoria genera with closely related arrays of species.

Molecular investigations of the phaneropterine genera *Monticolaria* Sjöstedt, 1909 and *Altihoratosphaga* Hemp (2009b) show that these taxa of forest and forest clearings speciated probably 0.5 to 0.9 million years ago, when a humid period connected high mountains with suitable vegetation (Hemp *et al.* 2009a, b). *Monticolaria* and *Altihoratosphaga* species occur on Mt Kilimanjaro, Mt Meru, the Manyara escarpment, and Mt Hanang. Species of both genera show very marked morphologically and molecularly detectable differences, while *Parasphena* species could not be separated by the same molecular methods and additionally morphological differences are small. Kevan (1956) says "many species of *Parasphena* appear to be very localized and often very closely related. Speciation is apparently in active progress, particularly under conditions of isolation on various East African mountains."

All *Parasphena* species still occupy analogous habitats (montane openland) found on mountains to heights of up to 4400 m (*P. pulchripes* on Mt Kilimanjaro), but rarely occurring below 1700 m (Table 1). This suggests that the distribution pattern of *Parasphena* in East Africa is the result of climatic regimes where suitable montane openland covered large areas of East Africa, enabling the ancestors to spread.

Besides *Parasphena*, present today on most high mountains of East Africa having openland in the montane zones, there are also

other Saltatoria species belonging to a typical "montane openland" coenosis. Members of this coenosis occur on most of the high mountains investigated (Table 2) and probably have spread during the same climatic conditions as *Parasphena*. Further investigation could show whether the present-day distribution of *Parasphena* is the result of periods of cold and dry conditions which are known to have prevailed, *e.g.*, during the last glacial maximum.

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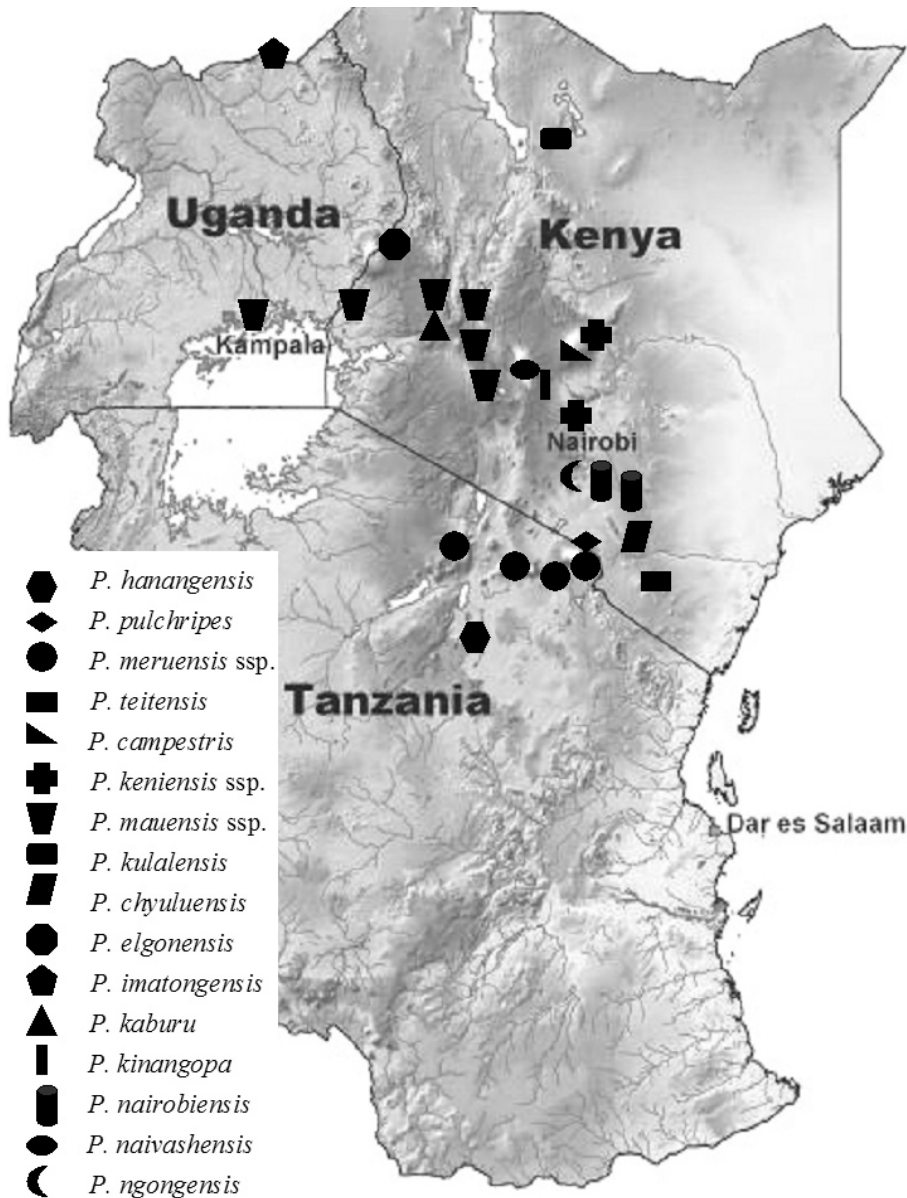


Fig. 4. Distribution of *Parasphena* in East Africa.

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